Branching in the Leafy Hepaticae.

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With thirty-six Figures in the Text.

THE branching of the shoot in the Hepaticae was carefully studied by Leitgeb ('71 *a*, '71 *b*, '72, '75) about forty years ago. Although most of the previous writers on this subject had confined their attention to a few thalloid genera, Leitgeb extended his observations to include a large number of leafy forms. He was able to demonstrate the fact that throughout the Jungermanniales (comprising the Metzgeriaceae and the Jungermanniaceae of many recent writers) the branches are never formed by a true dichotomy; that, in other words, the apical cell of a branching shoot never gives rise by a median longitudinal wall to the apical cells of two branches, a process which takes place in certain dichotomous Algae, such as *Dictyota*. In the Jungermanniales the branches invariably arise in segments cut off from the apical cell, and it is the persistence of the latter in the branching axis which indicates that the branching is monopodial in character.

Leitgeb showed further, however, that the apical cell of a future branch often made its appearance in an exceedingly young segment. Under these circumstances, if the branch grows vigorously and deflects the main axis to one side, the branch-system may simulate a dichotomy very closely. This is the case, for example, in *Metzgeria furcata* and in the genus *Bazzania* (Fig. 27). If, on the other hand, the branch grows less vigorously than the main axis and assumes a distinctly lateral position the branching is obviously of the monopodial type. *Riccardia multifida* and *Lepidozia reptans* (Fig. 8) may be cited as examples of this condition. When the branches arise close to the apical cell, as in the cases just considered, Leitgeb distinguishes the process as 'Endverzweigung' or 'Terminal Branching'. He contrasts with this 'Intercalary Branching', in which the branches first appear at some distance from the apical cell. In this latter type of branching the monopodial character is always apparent. It should be noted also that segments in which terminal branches begin their development are embryonic in character and are still undergoing cell-divisions; those where intercalary branches arise, on the other hand, have become more or less completely differentiated, and their cells have apparently ceased dividing.

Although Leitgeb's distinctions are based on differences in development, the two types of branches can usually be recognized in mature plants on account of the fact that terminal branches arise exogenously while intercalary branches arise endogenously. The result is that the superficial tissues of a terminal branch are continuous with those of the axis, while an intercalary branch shows a distinct sheath at its base formed by ruptured cortical tissues. In the present paper the branching in the Jungermanniaceae will alone be considered. This group, which is the equivalent of the Jungermanniae akrogynae of certain writers, includes the vast majority of the leafy genera and illustrates both terminal and intercalary branching much more fully than the other groups of the Hepaticae.

In order to give a clear idea of the way in which branches arise it will be necessary to describe briefly the normal divisions which take place in young segments. Here again our knowledge is largely based upon the work of Leitgeb. With the exception of the genus *Pleurozia*, where Goebel

FIGS. 1 and 2. Diagrams representing the sequence of segments cut off from apical cells.
Fig. 1. Spiral dextrospirale. Fig. 2. Spiral sinistrospirale.

('93, p. 453) has demonstrated a two-sided apical cell, the Jungermanniaceae all grow by means of a tetrahedral apical cell, which cuts off three longitudinal rows of segments in the usual way. On account of the orientation of the shoot one row of these segments will occupy a ventral position and the other two lateral positions (Fig. 1). When the segments are first cut off they are approximately in the form of flat triangular prisms, each bounded by two broad faces or walls and three narrow walls. One of the broad faces will lie in contact with the apical cell and may, as Leitgeb suggests, be designated the acroscopic wall; the other broad face, lying in contact with the next older segment of the same row, may then be distinguished as the basisopic wall. Of the three narrow faces one, the free wall, will be exposed at the apex of the shoot, while the two others will come into contact with segments of the two other rows. In the lateral segments these two narrow faces may be distinguished as the dorsal and ventral walls respectively. They may be distinguished also according to the direction of the spiral in which the leaves are arranged. In Fig. 1, for example, which represents a dextrospirale spiral, the dorsal wall in segment 4 is cathodic and the ventral wall anodic; in segment 3, on the other hand, the dorsal wall

is anodic and the ventral wall kathodic. In Fig. 2, which represents a sinistorse spiral, segment 4 agrees with segment 3 of Fig. 1 in having its dorsal wall anodic and its ventral wall kathodic, while segment 2 agrees with segment 4 of the same figure. Speaking generally, therefore, it may be stated that with a dextrorse spiral the anodic walls of the lateral segments will be ventral on the right-hand side (when a shoot is viewed from the ventral surface), while with a sinistorse spiral they will be ventral on the left-hand side. In the ventral segments the narrow enclosed walls are both lateral, but may be distinguished as anodic and kathodic. Of course the descriptive terms which have just been applied to the walls may also be applied to portions or regions of a segment.

The early divisions in a segment follow a definite sequence, and Leitgeb was therefore able to assign the branches which he studied to definite regions. In the lateral segments the first two walls are at right angles to

FIGS. 3 and 4. Diagrams representing the first two walls formed in a lateral segment and the establishment of the segment-halves.

the two broad faces. The first wall (Fig. 3, 1) extends from the middle of the free face to one of the enclosed narrow faces; the second wall (Fig. 4, 2) connects the first wall with the other narrow face. The segment thus becomes divided into an internal cell and two external cells, the latter being designated by Leitgeb the 'segment-halves'.¹ These halves may be distinguished as dorsal and ventral and also as anodic and kathodic. In the ventral segments the first wall brings about a division into an inner and an outer cell, the latter usually becoming subsequently subdivided by one or more anticlinal walls. In the further development of the shoot the internal cells of the segments are destined to give rise to the axial tissues of the stem, while the external cells will form the cortical tissues of the stem and also the leaves or other appendages. Each lateral segment develops normally a single leaf, which represents the entire breadth of the segment, and Leitgeb has clearly shown that in bilobed leaves the dorsal lobe has been formed from the dorsal segment-half and the ventral lobe from the ventral half. Even in leaves which are undivided at maturity the young rudiments show evidence of being bilobed, but the shallow sinus between them soon becomes obliterated. In leaves with more than two

¹ Leitgeb really applied the term 'segment-halves' to the two unequal cells formed by the first division wall in a lateral segment. The slight alteration in the application of the term, indicated above, makes it possible to homologize better the ventral segments with the lateral segments.

lobes one or both of the external cells of the young segment divide before the development of the leaf is clearly begun, and in this way the extra lobes are provided for. In the development of a leaf the segment-halves project and become divided by periclinal walls; these cut off the rudiment of the leaf from the cells which, by their further divisions, will form the cortical tissues of the stem. In ventral segments where underleaves are formed the development proceeds in much the same way.

Terminal Branching.

According to Leitgeb ('71 *b*) terminal branches always arise in the ventral portions of the lateral segments. He recognizes, however, two distinct kinds of terminal branching. In the first, which he describes as branching from a segment-half, the branch represents the entire ventral half of a segment, the apical cell of the branch making its appearance before the walls separating the leaf-rudiment from the cortical cells have been laid down. For the sake of convenience this may be designated the '*Frullania* type' of branching. In the second kind, which he describes as branching from the basisopic basilar portion of a segment, the apical cell of the branch arises in a cortical cell of the axis after the leaf-rudiment has been cut off. The branch represents therefore a much smaller portion of the segment than a branch of the first kind. Branching of the second kind may be distinguished as the '*Radula* type'.

About ten years ago the writer discovered in the Hawaiian genus *Acromastigum* ('00) a third kind of terminal branching, in which the branch represents a half of one of the ventral segments. No other representatives of this kind of branching have been discovered and it may be called the '*Acromastigum* type', although other kinds of branching occur in the same genus. A fourth kind of terminal branching, in which the branch represents the dorsal half of a lateral segment, is described below. It is known only in the subgenus *Microlepidozia* of the genus *Lepidozia*, and may therefore be characterized as the '*Microlepidozia* type'.

THE FRULLANIA TYPE.

Leitgeb ('71 *b*) describes the development of branches of this type very clearly, and his diagram of a sinistrorse branching axis, which is here reproduced in a slightly modified form (Fig. 5), illustrates the sequence of the early divisions. In segments 1 and 2 the ventral halves have each undergone four divisions, which have cut off the tetrahedral apical cells of the future branches. In fact each of these segment-halves is essentially an apical cell from the beginning, the three cells first cut off acting as the first three segments of the branch. It will be noted that the walls in the segment-halves are in the following sequence: the first wall extends from the first division wall of the segment to the acroscopic wall, meeting the

latter near its ventral extremity; the second wall extends from this first wall to the division wall, lying approximately parallel with the acroscopic wall; the third wall connects the first two walls. This sequence is the same in both segments, although segment 1 is situated on the right-hand side of the apical cell and segment 2 on the left-hand side, a difference which brings the branch in segment 1 in the kathodic segment-half and that in segment 2 in the anodic half. As Leitgeb points out further, this will make the spiral of the branch on the left-hand side sinistrorse, and therefore homodromous with that of the branching axis, while the branch on the right will be dextrorse and antidromous. If the branching axis were dextrorse the left-hand branch would still be sinistrorse and therefore antidromous, while the right-hand branch would be dextrorse and homodromous. In other words, the branches which arise in the anodic segment-halves are homodromous with the branching axis, those arising in the kathodic halves being antidromous.

Of course the relationships which have just been brought out remain equally evident after the axis and its branches have developed further, and it is usually quite possible, from the study of an older shoot, to recognize the *Frullania* type of branching at a glance and to refer the various appendages of the branch to their appropriate segments. As might naturally be expected, the first cell cut off from the segment-half gives rise to the first underleaf of the branch, the second cell to the

first lateral leaf (always situated on the side of the branch turned towards the apex of the branching axis), the third cell to the second lateral leaf (on the opposite side), the fourth cell to the second underleaf, and so on. With regard to the spirals, the branches on the left-hand side (when the shoot is viewed from the ventral surface) will all be sinistrorse and those on the right-hand side will all be dextrorse, whatever may be the direction of the spiral in the branching axis.

On account of the fact that a branch represents an entire ventral segment-half, only the dorsal half is left to form the leaf adjacent to the branch. This leaf consequently differs more or less from normal leaves, the most important differences being in form and in the number of lobes present. Sometimes, however, the leaf shows interesting peculiarities in its method of attachment. The leaves and underleaves at the base of a branch are also subject to more or less modification, both in form and in position. The differences in position are largely due to the fact that the first segments cut off from the original segment-half are less definitely

FIG. 5. Diagram representing the establishment of two branches of the *Frullania* type.

orientated than those which come later. Segment 1', for example, in Fig. 5, is not exactly ventral, but forms a considerable angle with the lower surface of the shoot, and segments 2' and 3' are also somewhat displaced. The differences in form are partly to be looked upon as reversions to a more juvenile condition, and partly as modifications associated with differences in environment.

The *Frullania* type of branching is more widely represented among the Jungermanniaceae than any of the other types of terminal branching. Some of the genera which show it have incubous leaves, some have succubous leaves, and some have complicate leaves. They include members of all the subfamilies recognized by Schiffner ('93-'95) with the exception of the Scapanioideae, the Stephanoideae (Raduloideae), and the Pleurozoideae. In certain genera, such as *Frullania*, *Porella*, and *Blepharostoma*, the branches all conform closely to this type; in other genera the *Frullania* type of branching occurs in connexion with other kinds. In *Bazzania*, for

FIG. 6. *Frullania Asagrayana*. Ledyard, Connecticut (A. W. E.). $\times 36$.

example, branches of the *Frullania* type and intercalary branches are both present, while in *Stictolejeunea* and a few other genera of the Lejeuneae terminal branches of both the *Frullania* type and the *Radula* type are developed. A number of characteristic examples of the *Frullania* type of branching will now be considered in detail. They are selected in order to show the modifications associated with the various methods of leaf-attachment.

Frullania.—The normal leaves throughout this genus are deeply complicate-bilobed, the dorsal lobe being much the larger of the two. The ventral lobe, or lobule, usually develops a hollow water-sac with the opening turned towards the base of the stem or branch. The underleaves are almost always bifid. The modifications usual at the base of a branch are clearly shown in *F. Asagrayana*, a common species of eastern North America. A fragment of a branching stem is represented in Fig. 6 with the base of the branch on the left-hand side, and it will be noted that both spirals shown are sinistorse. The incomplete leaf developed from the same segment as the branch consists of the dorsal lobe only; it spreads more obliquely than the other leaves, being almost symmetrically situated with respect to both stem and branch. The line of attachment (not shown in the figure) is partly on the stem and partly on the branch. The first underleaf of the branch is at the junction with the stem, and its line of attachment extends around the base of the branch until it almost meets the line of attachment of the incomplete leaf. Apparently, however, the

leaf is never coalescent with the underleaf. The latter is not essentially different in form from other underleaves, except that it frequently bears a small tooth at about the middle of its anodic edge. The first leaf of the branch is completely covered over by the incomplete stem leaf; it shows a well-developed lobule, usually in the form of a water-sac, but the dorsal lobe is very narrow and short, scarcely exceeding the lobule in length. The following leaves and underleaves are normal in structure and exhibit a gradual increase in size, rarely, however, becoming as large and as highly differentiated as the leaves and underleaves of the stem.

The modifications noted in *F. Asagrayana* are less striking than in certain other species of *Frullania*, and the remarkable *F. aculeata*, of western South America, may be chosen to illustrate a more pronounced specialization. In this species (Fig. 7) the first underleaf of the branch is divided to the very base. The anodic division is in the form of a slender subulate lamina, but the cathodic division is a well-formed water-sac, similar in all respects to those found on normal leaves. This water-sac, from its position, looks very much as if it belonged to the incomplete leaf, which covers over the base of the branch. The first leaf of the branch has a lobule in the form of a water-sac, just as in *F. Asagrayana*, but the dorsal lobe, instead of being a lamina, is also a water-sac of the same type. The development of three water-sacs at the base of a branch, where in most species a single one is found, is apparently associated with a more xerophytic habit. The condition seems to be especially frequent in species belonging to the subgenera *Meteoripsis* and *Diastoloba*.

FIG. 7. *Frullania aculeata*. Galapagos Islands (A. Stewart, No. 2770). $\times 17$.

Although in the two species just noted the first segment of a branch forms no appendicular organs except the first underleaf, Leitgeb ('75, p. 25) calls attention to the fact that in some species it often forms in addition short lobe-like appendages, which grow out between the underleaf and the incomplete leaf. These appendages, which are exceedingly variable even on an individual plant, are of considerable interest and help to explain certain peculiar structures found in other genera.

Lepidozia.—Only the subgenus *Eulepidozia* will be considered here, the discussion of *Microlepidozia* being deferred until the *Microlepidozia* type of branching is described. The common and widely distributed *L. reptans*, of

Europe, Asia, and North America, represents *Eulepidozia* adequately and is shown in Fig. 8. It will be noted that both stem and branch are dextrorse in the fragment drawn. The normal leaves in *L. reptans* are three- or four-cleft to about the middle, but the incomplete leaf at the base of a branch is only two-cleft, the apices of the lobes showing in the figure. This leaf is attached partly to the stem and partly to the branch, but is separated by a considerable distance from the first underleaf. The latter is usually bifid, although undivided or even trifid underleaves sometimes occur in this position. It is strongly concave and is inserted in such a way that the branch seems to arise in its axil. In fact, Stephani speaks of it as a sub-

FIG. 8. *Lepidozia reptans*. Huelgoat (Finistère), France (F. Camus). $\times 40$.

FIG. 9. *Sprucella succida*. N'dian, Kamerun (P. Dusén, Hep. Afr., No. 100). $\times 40$.

tending leaf ('91, p. 215). The sequence, however, shows clearly that it ought to be considered an underleaf, and this conclusion is supported by the fact that hyaline papillae are present at the apices of the lobes. In a leaf arising from a lateral segment there are no such papillae in the apical region. With the exception of the first underleaf the leaves of a branch show no special modifications, although a gradual increase in size is usually apparent.

Sprucella.—The genus *Sprucella* of Stephani ('91, p. 214), which includes the single African species *S. succida*, is closely allied to *Lepidozia*. The incubous leaves, which are almost longitudinally attached, are shortly bidentate at the apex, but are otherwise entire. The underleaves are much smaller; on robust stems they are nearly always quadrifid, but they may be only trifid or bifid. The terminal branching is essentially as in *Lepidozia*, but shows a few differences in detail. The incomplete leaf, for example,

which arises from the same segment as the branch (see Fig. 9), is much smaller than normal leaves and shows no indication of teeth, being merely acuminate at the apex. The first underleaf of the branch is so nearly ventral in position that it cannot be seen when the shoot is viewed from the dorsal surface. This underleaf is very minute and is undivided; it is subulate in form and is usually only four or five cells long and three cells wide at the base. The second underleaf of the branch is normal in structure, and the same is true of the other leaves.

In comparing *Lepidozia* with *Sprucella* Stephani remarks that one of the most important differences between the genera is in the insertion of the branches. He states that in *Lepidozia* a branch springs from the inner angle of a stem-leaf, which turns its concave surface towards the branch and thereby subtends it. In *Sprucella*, on the contrary, he describes the branch as springing from the outer angle of a stem-leaf, that is, from the angle which the ventral margin of the leaf forms with the stem. As the branch develops the leaf is said to be displaced to the dorsal surface of the stem and to appear partly on the stem and partly on the branch. He states further that there is no subtending leaf as in *Lepidozia*. It will be seen from the account given above that the branches in both genera spring from the outer angles of incomplete stem-leaves, belonging to the same lateral segments, and that the subtending leaf in *Lepidozia* is nothing more than the first underleaf of the branch, and is therefore homologous with the subulate underleaf at the base of the branch in *Sprucella*. If Stephani's figure is examined ('91, Pl. XXIX, Fig. 35) it will be seen that this diminutive underleaf in *Sprucella* did not escape his attention, because he shows it clearly in the first branch on the left. He makes no allusion to it, however, in his description.

Mastigophora.—The rare *M. Woodsii* of western Europe is a somewhat doubtful member of this genus because its organs of reproduction are still unknown. When compared with the species already considered it shows an interesting peculiarity in its branches connected with the method of attachment of the first underleaf. The leaves in *M. Woodsii* are deeply bifid, the ventral lobe being smaller than the dorsal and usually more or less deeply subdivided (Fig. 10). The lobes are connected by a rounded

FIG. 10. *Mastigophora Woodsii*. Moidart, Scotland (S. M. Macvicar). $\times 40$.

keel and tend to be slightly complicate. The underleaves are large and bifid. When a branch is formed the leaf arising from the same segment is broad but undivided (Fig. 11), and its line of attachment extends across the dorsal base of the branch. The first underleaf is remarkable because it is apparently not attached to the branch at all, but to the stem at some distance below the base of the branch. It seems to be laterally inserted on the stem, and its line of attachment is almost transverse as in ordinary underleaves. This underleaf is strongly concave, but when dissected off presents no unusual features either in form or size (Fig. 12). In such a case as this it must apparently be assumed that the base of the branch is coalescent with the stem. The description just given applies most forcibly to primary branches. When these become subdivided there is little or no coalescence at the base of a secondary branch, the first underleaf occupying much the same position as in *Lepidozia*.

FIGS. 11 and 12. *Mastigophora Woodsii*. Same material as Fig. 10.
Fig. 11. Incomplete leaf at base of branch. Fig. 12. First underleaf of branch. $\times 40$.

Pleuroclada.—Large and conspicuous underleaves are rarely associated with succubous leaves in the Jungermanniaceae. This condition, however, is found in *Pleuroclada albescens*, a widely distributed species of Europe and North America at high altitudes. The branching in this species is invariably of the *Frullania* type, and the structures at the base of a branch show a few distinctive features. Unfortunately the succubous insertion of the leaves, even here, is less distinct than in such genera as *Lophocolea* and *Chiloscyphus*, apparently on account of the fact that the bilobed leaves show a tendency to be complicate. If the line of attachment is examined it will be seen that the portion corresponding to the dorsal lobe is almost transverse, and that it is only in the portion corresponding to the ventral lobe that the obliqueness is clearly apparent. The leaves are strongly convex and appear almost hemispherical, the acute lobes being separated by a narrow sinus (Fig. 13). The underleaves approach the leaves in size, but are normally undivided and acute; their margins are either entire or unidentate on one or both sides. Two and sometimes three papillae can be demonstrated on an

underleaf, one at the apex and the others on the lateral teeth or in a corresponding position on the sides.

The leaf at the base of a branch shows its incomplete character by being undivided; its line of attachment extends until it almost meets the first underleaf, very much as in *Frullania*. In the figure only the apex and a portion of the base are visible. The first underleaf differs from ordinary underleaves in being distinctly bilobed, thus bearing a marked resemblance to a normal leaf arising from a lateral segment. It betrays its true nature, however, by the presence of a papilla at the apex of each lobe. The second underleaf of the branch is normal in form and position, and the other leaves show no striking peculiarities.

Lophocolea.—In this genus the leaves are distinctly succubous, and the underleaves are well developed, although relatively smaller than in *Pleuro-*

FIG. 13. *Pleuroclada albescens*. Valais Alps, Switzerland (F. Camus). $\times 40$.

FIG. 14. *Lophocolea heterophylla*. Stafford, Connecticut (G. E. Nichols). $\times 27$.

clada albescens. The branching is largely intercalary, but terminal branches of the *Frullania* type are not unusual. The plant chosen to represent this type of branching is a small and juvenile form of *L. heterophylla*, an exceedingly common species throughout Europe, Asia, and North America. In the portion of the plant shown in Fig. 14 it will be seen that the leaves are bifid and that the underleaves are either deeply bifid or quadrifid. The leaf which belongs to the same segment as the branch does not lie over the angle between the branch and the axis as in the species previously considered. It is situated instead below the branch, although its line of attachment extends nearly or quite to the base. The leaf is nearly as broad in the basal portion as normal leaves, but is undivided, the apex being sharply acuminate. The first underleaf of the branch is normal in position, and is often larger and more complex than the second underleaf. The first leaf is small but bifid, and is completely covered over by the leaves of the

branching axis which come after the incomplete leaf. The second and later leaves of the branch show a rapid progression in size. The modifications just described are shown equally well by *L. bidentata* (see Leitgeb, '75, p. 24), another species with an exceedingly wide distribution, and are doubtless to be found in other members of the genus.

Harpanthus.—The present genus is composed of two species, *H. Flotowianus* and *H. scutatus*, both of which are widely distributed in the Northern Hemisphere. According to the published descriptions the branching is invariably intercalary and ventral, and this statement is apparently true of *H. scutatus*. In robust forms of *H. Flotowianus*, however, branches of the *Frullania* type occasionally occur. The leaves of this

FIG. 15. *Harpanthus Flotowianus*. Riesengebirge, Bohemia (V. Schiffner, in Hep. Eur. Exsic., No. 294 b). $\times 17$.

FIG. 16. *Plagiochila frondescens*. East Maui, Hawaiian Islands (D. D. Baldwin, No. 85). $\times 17$.

species are decurrent and spread obliquely. They are distinctly succubous and are attached by an almost longitudinal line. The apex is very shallowly indented, the apical lobes or teeth varying from rounded to pointed. The much smaller underleaves are lanceolate and acute, and are sometimes unidentate on one or both sides. When a terminal branch is developed it shows a coalescence with the branching axis very much as in *Mastigophora Woodsii*, the first underleaf being apparently situated at some little distance from the base of the branch (Fig. 15). The incomplete leaf occupies much the same position as in *Lophocolea heterophylla*; it is nearly as large as the other leaves, but differs from them in being rounded and undivided at the apex. The first underleaf of the branch is considerably larger than normal underleaves and is deeply bifid with acute divisions.

The first leaf is almost transversely inserted and is much more symmetrical than the other leaves, the apical sinus being deeper and the lobes tending to be more acute. The other leaves and underleaves of the branch are not specialized.

Plagiochila.—The leaves in this genus are undivided, so that it stands in sharp contrast to the genera so far considered. Branching of the *Frullania* type is apparently restricted to species in which the secondary shoots are copiously subdivided and give rise to complex branch-systems. As an example *P. frondescens*, a widely distributed palaeotropic species, may be cited. The leaves in this plant (Fig. 16) usually show about half a dozen sharp teeth at the apex and along the ventral margin. They are attached by an oblique line which becomes abruptly arched at the ventral end. The underleaves consist of clusters of minute cilia bearing hyaline papillae. The incomplete leaf adjacent to a branch occupies the same position as in *Lophocolea* and *Harpantus Flotowianus*; it is somewhat narrower than the other leaves, but is much like them in other respects and is attached by a line of the same type. The first underleaf of the branch is slightly displaced towards the basiscopic side (with respect to the branching axis), but shows no other modifications. The first leaf is more or less reduced in size, being sometimes very small indeed. In the example figured it appears as a lanceolate, entire lamina, but it is subject to variation and is often toothed. The succeeding branch-leaves are essentially like other leaves.

In the genus *Chiloscyphus*, as recently restricted by Schiffner ('10), branches of the *Frullania* type are not infrequent. They agree closely with those just described for *Plagiochila frondescens* and, like them, are usually associated with leaves which are undivided at maturity. Müller, however, refers these branches to the *Radula* type ('06-'11, p. 818).

Lophozia.—With the exception of subfloral innovations branches are difficult to demonstrate in most species of *Lophozia*. Terminal branches of the *Frullania* type, however, have been recognized in *L. inflata* and *L. acutiloba*, two species which Müller ('06-'11, p. 738) separates from *Lophozia*, reviving for them the old generic name *Gymnocolea*. Müller (p. 675) has also noted the exceptional occurrence of such branches in *L. longiflora*, var. *uliginosa*, and in *L. Wenzelii*, while the writer has been able to demonstrate them in several other members of the genus, some belonging to the subgenus *Dilophozia* and some to the subgenus *Barbilophozia*. As an example of *Dilophozia*, *L. Wenzelii*, an alpine and arctic species of Europe, Asia, and North America, will be described. The leaves are distinctly succubous and have a shallow apical sinus with broad and bluntly pointed lobes. The line of attachment is long and oblique and the leaves are normally plane or nearly so. Underleaves are represented by minute hair-like structures tipped with hyaline papillae and are usually short-lived and difficult to

demonstrate. Fig. 17 shows a branch of the typical *Frullania* type. It will be noted that the leaf belonging to the same segment as the branch is similar to the other leaves, but is undivided, and that the line of attachment comes to an end at some little distance from the base of the branch. The first underleaf is a distinct though small lamella, and the first leaf of the branch differs from normal leaves in being somewhat complicate. The modifications are comparable with those seen in *Harpanthus Flotowianus*, although there is no marked coalescence between the branch and the axis.

In Fig. 18 an interesting variation is shown, in which the incomplete leaf is attached by a line which seems to be prolonged as far as the first underleaf of the branch. The part adjacent to the underleaf corresponds

FIGS. 17 and 18. *Lophozia Wenzelii*. Near Hallen (Jemtland), Sweden (H. W. Arnell and A. Grape, in Hep. Eur. Exsic., No. 172). $\times 17$.

to a sharp lobe-like tooth, which is united to the leaf at its ventral base. This tooth might perhaps be considered the first underleaf of the branch; it might be considered an accessory lobe of the incomplete leaf; it might be considered an appendage of the first segment of the branch, borne in addition to the first underleaf and similar to the appendages described by Leitgeb in *Frullania*. The first interpretation is hardly permissible, because a minute underleaf very much like the one shown in Fig. 17 is visible at the base of the tooth; there are also objections to the second interpretation on account of the long line of attachment; the third interpretation, however, seems to accord well with the conditions present. An examination of Fig. 5 shows that the first segment of the branch and the dorsal segment-half are adjacent, so that a coalescence between the

appendicular organs which spring from these regions would not be at all surprising. Similar unions, in fact, are frequently met with between bracts and bracteoles and are not unusual between ordinary leaves and underleaves.

As members of the subgenus *Barbilophozia*, *L. attenuata* and *L. Floerkei* may be considered. Both of these species are widely distributed in the northern parts of Europe, Asia, and North America. In *L. attenuata* the leaves are commonly trifid, although bifid leaves are not unusual. They are attached by an oblique line, but often show more or less tendency to be complicate, the dorsal lobe being connected with the rest of the leaf by a rounded keel. Sometimes the dorsal portion is attached by an almost transverse line. The underleaves are minute and inconspicuous, and were not made out in the material studied on account of the thick felt of rhizoids. When a branch is developed (Fig. 19) the leaf belonging to the same segment is undivided and acute, corresponding clearly to the dorsal lobe of an ordinary leaf. At some little distance from the incomplete leaf, on the ventral surface of the shoot, another leaf-like structure, which is also undivided and acute, can be discerned. This should apparently be interpreted as an appendage of the first segment of the branch but distinct from the first underleaf. It differs from the homologous appendage in *L. Wenzelii* in being entirely free from the incomplete leaf. The first branch-leaf in *L. attenuata* is small and often undivided; it is usually covered over by the next stem-leaf on the same side as the branch. The remaining leaves of the branch show no special modifications.

A study of *L. Floerkei* adds further support to the interpretation just given of *L. attenuata*. The leaves in *L. Floerkei* are normally trifid and the distinct underleaves are bifid.

At the base of a branch a structure like that shown in Fig. 20 can be demonstrated. The first underleaf of the branch (at the left-hand end of the figure) is similar to the other underleaves, but is undivided; the incomplete leaf is also undivided and clearly represents a dorsal lobe; between the two and somewhat coalescent with the leaf is a broad bifid structure, which is evidently homologous with the lobe-like tooth

FIG. 19. *Lophozia attenuata*. Helsingfors, Finland (H. Lindberg, in Hep. Eur. Exsic., No. 95). $\times 40$.

FIG. 20. *Lophozia Floerkei*. Bethesda, Wales (W. H. Pearson). $\times 27$.

described in *L. Wenzelii*. The examples just considered thus form a kind of series with respect to the structures at the base of a branch. In Fig. 17 of *L. Wenzelii* the first ventral segment of the branch has formed simply the first underleaf; in Fig. 18 of the same species it has formed in addition a small appendage coalescent with the incomplete leaf; in *L. Floerkei* the appendage is much larger and the coalescence is less extensive; in *L. attenuata* the appendage is also large, but is entirely free from the leaf. In all probability an extensive study of the species here considered and allied species would show more or less variation in the structures described.

The branches in *L. inflata* and *L. acutiloba* offer a few further points of interest. *L. inflata* is one of the most widely distributed and variable

FIG. 21. *Lophozia inflata*. Riesengebirge, Bohemia (V. Schiffner and E. Bauer, Bryoth. Bohem., No. 294). $\times 17$.

FIG. 22. *Lophozia inflata*. Same material as Fig. 21. $\times 17$.

species in northern Europe, Asia, and North America; the closely related *L. acutiloba*, on the other hand, is known from only a few European localities. Schiffner ('03, p. 28) states that in *L. inflata* the leaf developing from the same segment as a branch is undivided, thus differing from the normal two-lobed leaves, and he also makes similar statements about *L. acutiloba* ('09). In Fig. 21, which represents a robust aquatic form of *L. inflata*, the conditions described by Schiffner are clearly shown. The normal leaves are here somewhat more explanate than in some of the other forms of the species; they show a long oblique line of attachment and two rounded lobes separated by an obtuse sinus. The incomplete leaf is at some little distance below the branch; it is attached by a shorter line and is merely rounded at the apex. The leaves of the branch are essentially normal

from the beginning. In the form figured there are no distinct underleaves, the only ventral appendages being hyaline papillae which sometimes cut off a few cells at the base. A group of these papillae can usually be distinguished at the base of a branch in the position where an underleaf would naturally appear.

In addition to the branches just discussed, Müller, in both *L. inflata* and *L. acutiloba*, describes cases in which the leaf below the branch is bilobed instead of being undivided. This condition does not seem to be infrequent and is shown in Fig. 22. It will be seen that the leaf below the branch (the lower leaf on the right-hand side) looks like the other leaves except that its line of attachment is shorter. If it were not for this slight difference and for the difference in the sequence in which the leaves are borne, it would be difficult to distinguish the branch from the branching axis. Müller refers branches like this to the *Radula* type instead of to the *Frullania* type. There are, however, two objections to this interpretation: first, the sequence in which the leaves of the branch are borne, and, second, the short line of attachment of the leaf below the branch. In the writer's opinion the branches shown in the two figures of *L. inflata* ought both to be referred to the *Frullania* type. The presence of two lobes in one of the incomplete leaves could then be ascribed to the tendency, which so many species of *Dilophozia* show, to develop more than the normal number of lobes. The terminal branches in *L. acutiloba* are in all essential respects like those of *L. inflata*.

FIG. 23. *Jamesoniella autumnalis*. Cromwell Connecticut (A. W. E.). $\times 17$.

Jamesoniella.—In *J. autumnalis*, a species which is aberrant in certain respects, branching of the *Frullania* type can occasionally be observed. In all typical members of the genus the branches are apparently always intercalary and ventral. *J. autumnalis* is widely distributed throughout North Temperate regions. The leaves (Fig. 23) are undivided and rounded, and the line of attachment is long and oblique. The minute underleaves are often short-lived and difficult to demonstrate among the rhizoids. The incomplete leaf at the base of a branch is coalescent with a lobe-like appendage at the ventral base, similar to the one figured in *Lophozia Wenzelii*. The appendage varies considerably in size and in the extent of coalescence; the apex varies also from acute (as shown in the figure) to obtuse or rounded. The first underleaf of a branch tends to be a trifle larger than normal underleaves, but the other branch-leaves show no modifications of interest.

Zoopsis.—Among the genera which Spruce ('82) included under *Cephalozia*, branching of the type now being discussed seems to be exceedingly rare. It has been reported, in fact, in scarcely a half-dozen species, two of which belong to the genus *Zoopsis* and the others to the genus *Cephalozia* in its restricted sense (the subgenus *Eucephalozia* of Spruce). In *Zoopsis* Leitgeb ('76) alluded briefly to the branching and stated that only vegetative branches ever conformed to the *Frullania* type. His observations were largely based on *Z. argentea*, a widely distributed species the range of which extends from New Zealand and Australia into tropical Asia. The leaves in this species are probably the most rudimentary found in the genus (Fig. 24). Each consists of only four cells, two of which form the base. The other two cells are in the form of papilla-like appendages attached more or less trans-

FIG. 24. *Zoopsis argentea*. New Guinea (L. Loria, No. 63). $\times 80$.

versely to the basal cells, the one belonging to the more dorsal cell being about twice as long as the other. Although at first sight the leaves appear longitudinally inserted, they are really very slightly succubous. The underleaves are minute, but are apparently always present. In the figure the branch is on the right-hand side, and it will be seen that the leaf belonging to the same segment consists of only two cells, the long apical papilla indicating that the dorsal half is the one represented. It should also be noted that this incomplete leaf seems to be situated at the base of the branch instead of on the branching axis. Aside from this peculiar leaf there is little to show that the branch-system is not a dichotomy, the first leaf of the branch being normal in structure and position

and the first underleaf (not shown in the figure) being ventral and like the other underleaves of the plant.

Cephalozia.—The *Frullania* type of branching has been noted by Leitgeb ('75) in *C. bicuspidata* and *C. curvifolia*, by Spruce ('82) in *C. tubulata*, and by Stephani ('06-'09) in *C. hamatiloba* and *C. asperrima*. Only the first two of these species will be considered here. They are both widely distributed in Europe, Asia, and North America. In *C. bicuspidata* Leitgeb calls attention to the undivided leaf at the base of a branch and notes that he has observed branching of this type in but a single instance. Apparently, however, the phenomenon is less uncommon than he implies. The writer has found it to occur not infrequently in specimens from British Columbia collected by Macoun and by Brinkman, and also in a specimen from Baden collected by Jack and distributed in Gottsche and Rabenhorst's *Hepaticae Europaeae* (No. 353). In Fig. 25, which represents one of

Macoun's plants, it will be noted that the sharply bilobed leaves are distant and tend to be somewhat complicate. The dorsal lobe is almost transversely inserted, but the line of attachment of the ventral lobe is distinctly oblique, the conditions being much the same as in *Pleuroclada albescens*. No underleaves are present, each ventral segment bearing instead a single hyaline papilla. The incomplete leaf at the base of the branch is undivided and acuminate. The first segment of the branch bears a hyaline papilla (not visible in the figure) and, in addition, a large leaf-like appendage. Apparently there is never coalescence between the appendage and the incomplete leaf, although their lines of attachment sometimes approach each other very closely. The branches in this plant bear a strong resemblance to those described in *Lophozia attenuata*.

FIG. 25. *Cephalozia bicuspidata*. Ucluclet, British Columbia (J. Macoun, No. 115). $\times 40$.

FIG. 26. *Cephalozia curvifolia*. Franconia Mountains, New Hampshire (A. W. E.). $\times 40$.

In *C. curvifolia* (sometimes made the type of the distinct genus *Nowellia*) branching of the *Frullania* type is not unusual. The leaves in this species are attached in much the same way as in *C. bicuspidata* and are characterized by the strongly inflated base of the ventral lobe (Fig. 26). The ventral segments produce hyaline papillae, just as in *C. bicuspidata*. The leaf at the base of a branch, lacking the ventral lobe, is reduced to a narrow lanceolate lamina with a very short line of attachment. The first segment of the branch bears a hyaline papilla, but no leaf-like appendage, thus differing markedly from *C. bicuspidata* and agreeing with such species as *Lophozia inflata* and *L. acutiloba*.

Bazzania.—The terminal branching in *Bazzania*, which conforms closely

to the *Frullania* type, exhibits a number of interesting peculiarities. The modifications which occur at the base of a branch are shown in Fig. 27, which represents *B. tricrenata*, a widely distributed species in the northern and mountainous regions of Europe, Asia, and North America. The spirals shown in the figure are both dextrorse, and it will be noted that the distance between a leaf on the right-hand side and the next underleaf is much less than the distance between the underleaf and the next leaf on the left-hand side. An occasional leaf in *B. tricrenata* is bluntly tridentate at the apex, but most of the leaves diverge from this typical condition. The underleaves are broader than long, and are either entire or irregularly toothed or lobed at the apex. The incomplete leaf at the base of a branch is always undivided at the apex and acute, and its line of attachment, as in similar cases, is partly on the stem and partly on the branch. The

FIG. 27. *Bazzania tricrenata*. Beacon Falls, Connecticut (A. W. E.). $\times 27$.

first underleaf of a branch is smaller than the other underleaves and tends to be distinctly bilobed; it is displaced in such a way that its line of attachment almost reaches that of the next underleaf in the stem-spiral. The first leaf of the branch is small, but the later leaves and underleaves show no special modifications.

In the genera previously considered the branches have been partly on one side of the main axis and partly on the other. This has made the branching axis and the branch sometimes homodromous and sometimes antidromous. In *Bazzania*, however, Leitgeb ('71 *b*) brings out the fact that the spirals in a branch-system are invariably homodromous, although in some plants they may be dextrorse and in others sinistrorse. He shows that this condition is due to the restriction of the branches to anodic segment-halves. This being the case a dextrorse branching axis would develop branches on the right-hand side only (when viewed from the ventral surface) and a sinistrorse axis on the left-hand side. On account of the simulated dichotomy in *Bazzania* the shoot-system never appears one-sided, as it necessarily would if an obvious monopodium were maintained.

From the standpoint of comparative morphology Velenovský ('05, p. 112) concludes that terminal branching, especially of the *Frullania* type, represents a true dichotomy. In his opinion evidence derived from developmental study is of no value in deciding questions of this kind. Unfortunately he fails to give reasons for his opinion in this particular case. It cannot be based upon the fact that the two new axes which result from

the branching are alike in all respects. Even in *Bazzania*, where the dichotomous appearance is so strongly marked, the branch can at once be distinguished from the branching axis by comparing the sequences of the leaves. It will be seen in Fig. 27, for example, that the spiral in the branch (on the right) is not continuous with that of the main axis below the branch, while the spirals in the two portions of the main axis (below and above the branch) are continuous. Of course, in such a genus as *Frullania*, the differences between a branching axis and a branch are still more striking.

According to Servit ('07), who accepts Velenovský's idea of a dichotomy, the genus *Bazzania* does form two equivalent new axes, and his Fig. 1, representing the common *B. trilobata*, seems to support his assertion. A close scrutiny of this figure, however, will show that it is incorrect and that, in the axis on the left (the main axis), the leaf on the left-hand side should precede and not follow the leaf on the right-hand side. In other words, the spirals ought to be homodromous and not antidromous, as the figure indicates and as a true dichotomy would require. Servit goes so far as to homologize the incomplete leaf in *Bazzania* (and in other genera showing the *Frullania* type of branching) with the 'Angularblatt' which Velenovský describes in the dichotomous Pteridophytes ('05, p. 249). He states that an 'Angularblatt' is distinguished from other leaves by its form, by its position in the angle formed by a dichotomy, and by its being attached equally to the two new axes. His characterization applies in all essential respects to many Jungermanniaceae with incubous or complicate leaves, but breaks down more or less in genera with succubous leaves. In *Lophocolea*, for example, the incomplete leaf is situated below the branch and shows no relation to the angle between the branch and the main axis. On the whole it seems unnecessary to consider the incomplete leaf as a special morphological modification; it would certainly be simpler to regard its peculiarities as due to the restricted portion of the segment which takes part in its formation.

THE MICROLEPIDOZIA TYPE.

The condition of homodromy which *Bazzania* secures through the suppression of branching on one side of a branching axis is secured by the subgenus *Microlepidozia* in a different way, an obvious monopodium with homodromous branches on both sides being the result. Here, as in *Bazzania*, the branches are restricted to the anodic segment-halves, but while this brings them in the ventral segment-halves on one side of a branching axis it brings them in the dorsal segment-halves on the other. This remarkable peculiarity of *Microlepidozia* is clearly illustrated by *Lepidozia setacea*, a widely distributed species in northern Europe and North America. In Fig. 28 a portion of a dextrorse axis with two branches is shown, and it will be

noted that both branches are dextrorse also, that the branch on the right-hand side has arisen in a ventral segment-half, and that the branch on the left has arisen in a dorsal segment-half. In other words, the branch on the right conforms to the *Frullania* type and that on the left to the *Microlepidozia* type.

FIG. 28. *Lepidozia* (*Microlepidozia*) *setacea*. Franconia Mountains, New Hampshire (A. W. E.). $\times 100$.

When the branching in *Microlepidozia* was first studied by the writer ('04, p. 187) it was observed that, looking at a branch-system from the dorsal surface, none of the branches on one side had incomplete leaves at the base while all the branches on the other side showed such leaves clearly. The conclusion was reached that the branches without incomplete leaves represented entire segments, thus leaving nothing for the formation of leaves. Further study, however, has brought out the fact that this interpretation is incorrect and that these branches have incomplete leaves at the base just as

in the *Frullania* type, the only difference being that they are situated on the ventral surface of the shoot instead of on the dorsal. It will be seen from

FIG. 29. Diagram representing the establishment of a branch of the *Microlepidozia* type on the left and one of the *Frullania* type on the right.

the figure that the first branch-leaf in the *Microlepidozia* type is not an underleaf, as in the *Frullania* type, but a lateral leaf on the side of the branch turned away from the main axis, that the second leaf also is a lateral leaf but on the other side, and that the third leaf represents the first underleaf formed. None of these branch-leaves show special modifications. Sinistrorse branching systems as well as dextrorse may be observed in *Microlepidozia* just as in *Bazzania*.

The accompanying diagram (Fig. 29) illustrates the terminal branching in *Microlepidozia*. The oldest segment on the right shows the *Frullania* type and agrees with Fig. 5; the segment on the left shows the establishment of the apical cell of a branch in the dorsal segment-half, according to the *Microlepidozia*

type. It will be noted that the segments on this side follow the same sequence as on the other side and correspond with the leaves and underleaves described above. In addition to terminal branching *Microlepidozia* shows intercalary branching from ventral segments.

THE ACROMASTIGUM TYPE.

The genus *Acromastigum* contains the single Hawaiian species *A. integrifolium*. Since a detailed description of the branching in this plant has already been published by the writer ('00), only the more essential features of the *Acromastigum* type will be mentioned here. The species shows in addition terminal branching of the *Frullania* type and ventral intercalary branching. In the development of a ventral segment the first wall laid down is periclinal and gives rise to an internal and an external cell, the latter soon dividing by an anticlinal wall into two cells or segment-halves. If the development continues in the usual way one of the external cells again

FIG. 30. Diagram representing the establishment of a branch of the *Acromastigum* type on the right and one of the *Frullania* type on the left.

divides by an anticlinal wall, so that the segment shows three external cells. These three cells give rise to three hyaline papillae, which are carried forward on the apex of the underleaf developed from the segment. When a terminal branch is to be formed from a ventral segment the apical cell of the branch becomes differentiated in one of the segment-halves, leaving a single external cell for the underleaf. The result is that the underleaf is much narrower than usual and shows only one apical papilla. The branch is situated at one side of this narrow underleaf, sometimes on the right and sometimes on the left. In Fig. 30 the establishment of a branch of this character is shown diagrammatically on the right-hand side, while a branch of the *Frullania* type is shown in the lateral segment on the left. The first two segments cut off in the ventral branch give rise to lateral leaves and the third to an underleaf. It will be noted that the spiral is sinistrorse in the branch figured; if the branch had been on the left-hand side the spiral would have been dextrorse. The same thing would have been true if the spiral of the main axis had been dextrorse instead of sinistrorse. In other words, the branches arising in anodic segment-halves are homodromous with the main axis, while those arising in cathodic segment-halves are antidromous, the relation being the same as in branching of the *Frullania* type. Branches of the *Acromastigum* type are apparently always flagelliform, and their minute leaves and underleaves present no modifications of special interest.

THE RADULA TYPE.

The *Radula* type of terminal branching was the one first described by Leitgeb ('71 a) and has already been briefly characterized. It has sometimes been referred to as the '*Lejeunea* type' by the writer ('07, '08). On account of the late differentiation of the apical cell of a branch, the leaf belonging to the same segment is normally developed and shows none of the interesting peculiarities described under the previous types of terminal branching. As Leitgeb points out, a branch of the *Radula* type always arises in a cortical cell adjacent to the base of a leaf on the basiscopic side and in the ventral portion of the segment. In the genus *Radula* the branches all conform to this type, and it is also found throughout the vast group of the Lejeuneae. In most of the genera of this group the branching is entirely of the *Radula* type. In a few genera of the Lejeuneae Holostipae, however, such as *Stictolejeunea* and *Bryopteris*, branching of the *Frullania* type also occurs. These genera, together with the related genus *Jubula* (in which likewise both types of branching are found), have already been discussed by the writer in other connexions ('07, '08). Whether the *Radula* type of branching occurs in other members of the Jungermanniaceae is doubtful, although Leitgeb assigns it to *Scapania* ('75, p. 29), Goebel to *Anomoclada* ('06, p. 130), and Müller to *Lophozia inflata*, *L. acutiloba*, and *Chiloscyphus* ('06-'11). The terminal branching in *Lophozia* and *Chiloscyphus*, as interpreted by the writer, has been described under the *Frullania* type, and the branching in *Scapania* and *Anomoclada* will be considered in connexion with intercalary branching.

The development of the branches in *Radula* and the Lejeuneae is treated by Leitgeb at considerable length, but his statements with regard to the sequence of the segments in the branch-rudiments are not altogether consistent. This is probably due to the fact that the sequence conforms less rigidly to rule than in the other types of terminal branching, a condition clearly brought out by a comparison of fully developed shoots. In describing *Radula* ('71 a, p. 37) he states that the first segment of the branch is basiscopic (with respect to the main axis), the second acroscopic, and the third ventral. This would bring the first branch-leaf on the side of the branch turned away from the apex of the main axis, in marked contrast to what is found in the *Frullania* type. It would also make the spirals of the branches on the left-hand side of the axis dextrorse and those on the right-hand side sinistrorse. In describing the Lejeuneae, however, he states that the first branch-leaf is an underleaf ('75, p. 28). This would imply that the first segment of the branch instead of the third was ventral in position. Even under these circumstances, if the first lateral leaf retains its basiscopic situation, the branches on the left-hand side would still be dextrorse and those on the right-hand side sinistrorse. The examination of a branch in

Radula (Fig. 31) or in one of the *Lejeuneae* (Fig. 32) shows that his statements with regard to the lateral leaves are correct, the first leaf being constantly basispic. The spirals, however, show certain deviations. The determination of a spiral in *Radula* is beset with difficulties because the ventral segments bear no appendages. It is only by studying the apical cell and the young segments that the direction of the spiral can be positively demonstrated. This was done in the species figured, *R. aquilegia* of western Europe, and it was found that the branch-spirals on the left-hand side of a branching axis were sinistrorse instead of dextrorse as Leitgeb's account demands. This would, of course, make the ventral segment in the branch-rudiment second instead of third in the sequence, the basispic segment still being first. The conditions just described are found in both vegetative branches and subfloral innovations and are apparently constant throughout the genus.

FIG. 31. *Radula aquilegia*. Moidart, Scotland (S. M. Macvicar). $\times 27$.

FIG. 32. *Euosmolejeunea duriuscula*. Sanford, Florida (S. Rapp). $\times 40$.

In most of the *Lejeuneae* underleaves are present, so that the determination of a spiral is an easy matter. It is necessary here to distinguish between subfloral innovations and vegetative branches because they sometimes show differences which are not to be found in *Radula*. In the species figured (Fig. 32), *Euosmolejeunea duriuscula* of tropical and subtropical America, the peculiarities and variations of the innovations are well shown. It will be seen that the innovation on the right conforms closely to Leitgeb's conception, the first branch-leaf being an underleaf, the first lateral leaf being basispic, and the spiral being sinistrorse. The innovation on the left, however, is also sinistrorse, the first leaf being basispic and the underleaf being second in the sequence. A study of numerous innovations has shown that there is apparently no relation between their spirals and the spiral of the flowering axis, although the condition shown by the left-hand innovation seems to be much commoner than the other. This condition is of course identical with what has just been described for *Radula*.

In the vegetative branches the differences noted in the innovations do not seem to occur. In a large series examined the spirals were all found to agree with those in *Radula*. It may be stated, therefore, that in the *Radula* type of branching the spirals usually run in the same direction as in the *Frullania* type, dextrorse branches being on the right-hand side of a branching axis and sinistrorse branches on the left-hand side. In the *Radula* type, however, the first underleaf (or first ventral segment) comes second in the sequence instead of first.

Although the branches in *Radula* and the innovations in the Lejeuneae are clearly exogenous, the exogenous nature of the vegetative branches in the Lejeuneae is less apparent, each branch bearing at its base a sheath which seems at first sight to be composed of ruptured cortical tissue. The common *Lejeunea cavifolia*, of Europe, Asia, and North America (Fig. 33),

FIG. 33. *Lejeunea cavifolia*. Huelgoat (Finistère), France (F. Camus). $\times 40$.

may be chosen to illustrate the conditions present. According to Leitgeb ('75, p. 28) this sheath is really composed of the first leaf-cycle of the branch, the first underleaf and the first two lateral leaves having coalesced by their margins. The leaves are very rudimentary and form at first a covering through which the developing branch must push its way. In favourable cases he was able to demonstrate the boundaries between the leaves. He associates these foliar sheaths with the fact that the branches in the Lejeuneae, although laid down near the apex, often remain latent for a considerable period.

Leaving the foliar sheaths out of consideration, the first leaves on branches of the *Radula* type show less definite modifications than in the other types of terminal branching. They are usually smaller than normal leaves, and their lobules (ventral lobes) are often very rudimentary. The first underleaves, also, are sometimes smaller and less complex than those afterwards formed. In most cases there is a transition, sometimes very gradual, between the basal leaves and the more typical leaves which the branch later develops. The modifications present may be looked upon as reversions to a more juvenile condition.

Intercalary Branching.

Terminal branching of the *Radula* type, as Leitgeb intimates, is intermediate in certain respects between terminal branching of the *Frullania* type and intercalary branching. In the *Frullania* type (and the same thing is true of the *Microlepidoxia* and *Acromastigum* types) the branches arise very close to the apex, their leaves follow a definite sequence, the branch-spirals conform to definite rules, and the exogenous origin is perfectly clear.

In the *Radula* type the formation of the branches is longer delayed, the sequence of the branch-leaves is less definite, the spirals conform less rigidly to rule, and, in the vegetative branches of the *Lejeuneae* at least, basal sheaths are present, whatever the morphological nature of these sheaths may be. In intercalary branching the formation of the branches is still longer delayed, the sequences of the branch-leaves are indefinite, the spirals show no conformity to rule, and the basal sheaths are constant and evidently represent ruptured cortical tissue. The peculiar features of intercalary branches are illustrated below by concrete examples.

According to Leitgeb ('72, '75) intercalary branches almost invariably arise in ventral segments. Even in cases where they appear lateral he considers that they are probably ventral in origin but displaced through subsequent inequalities of growth. The only case in which he assigns intercalary branches to lateral segments is in *Jubula Hutchinsiae*, a rare species of western Europe ('75, p. 36). In this plant the vegetative branches conform closely to the *Frullania* type and the subfloral innovations to the *Radula* type. The branches which he regards as intercalary are the short male branches, which are situated behind normal leaves, bearing the same relation to them as the subfloral innovations do to the perichaetial bracts. His opinion is based upon the fact that each branch has a distinct basal sheath, and, since he was unable to demonstrate the boundaries of coalesced leaves and saw in the sheaths evidence of active cell-division, he concluded that they represented cortical tissue. Unfortunately his explanation and figure are not convincing, and there seems to be no imperative reason why these sheaths should not be interpreted in the same way as the very similar sheaths in the *Lejeuneae*.

Although this doubtful case is the only one recognized by Leitgeb, the writer would refer certain intercalary branches in a number of species to lateral segments rather than to ventral. This course seems justifiable from the position which these branches occupy on adult shoots, although it has unfortunately been impossible to trace out their development from the earliest beginnings or to assign them to definite portions of the original segments. The genera where branches of this kind occur are the following: *Micropterygium*, *Diplophyllia*, *Scapania*, *Sphenolobus*, *Cephaloziella* (subgenus *Prionolobus*), *Odontoschisma*, *Anomoclada*, *Plagiochila*, and *Chiloscyphus*. In all probability this list could be considerably increased. As an illustrative example of lateral intercalary branching the genus *Micropterygium* of tropical America may be selected. In *M. Pterygophyllum*, a widely distributed species (Fig. 34), the large underleaves are very much like those of *Bazzania*, but the lateral leaves show a very peculiar structure. They are distinctly complicate, but only the dorsal lobe is attached to the axis, the ventral lobe being formed by a folding back of its lower margin. Along the keel thus formed, in well-developed leaves, a wing of variable

extent may be seen. The branches are situated in the axils of the leaves and show a distinct basal sheath. In the majority of cases, as in the branch on the right, the first leaf is basispic with respect to the main axis, the second leaf is an underleaf, and so on. In the figure the first leaf is only partially visible and is considerably displaced from its theoretical position. In the branch on the left it will be noted that the first leaf is acroscopic, and cases may also be found where the first leaf is an underleaf. The main axis in the figure is sinistrorse, the branch on the right is dextrorse. Other cases were observed, however, in which dextrorse spirals occurred in branches on the left and sinistrorse spirals in branches on the right. So far as can be learned the spiral of the main axis exerts no influence upon the spirals

FIG. 34. *Micropterygium Pterygophyllum*.
Mabess River, Jamaica (A. W. E., No. 316). $\times 40$.

FIG. 35. *Plagiochila Sullivantii*.
Quarry Run, West Virginia (A. L. Andrews). $\times 17$.

of the branches. In the genera *Scapania*, *Diplophyllia*, *Sphenolobus*, and *Cephaloziella* (subgenus *Prionolobus*) the leaves are bilobed and more or less complicate, but their lobes are both attached to the axis. With the exception of certain species of *Cephaloziella* none of these genera produce underleaves. Their lateral intercalary branches are distinctly axillary and resemble in most essential respects the branches of *Micropterygium*.

The other genera, where lateral branches are here interpreted as intercalary, are all distinguished by succubous undivided leaves. *Plagiochila Sullivantii*, a species of the eastern United States, shows the usual conditions present (Fig. 35). The branch figured is borne in the axil of a leaf but close to the ventral margin, and an examination of *Chiloscyphus* will show that the female branches arise in much the same position. Apparently in branching of this kind there is more or less variation in the relative positions

of leaf and branch, although the latter may always be described as axillary. In the common *Plagiochila asplenoides*, for example, Servit ('07, Fig. 3) figures a branch much nearer the middle of a leaf than is shown above, while in the South American *Anomoclada mucosa*, as well as in certain species of *Odontoschisma*, the lateral branches are close to the dorsal margins of the leaves. In all these cases, so far as examined, the branch-spirals and the sequences of the branch-leaves exhibit as great an irregularity as in *Micropterygium* and the other genera with complicate leaves.

The ruptured cortical sheath at the base of a lateral intercalary branch is usually conspicuous, but aside from this the basal structures show no very striking modifications. In most cases the first few cycles of leaves are rudimentary and often more or less displaced from their theoretical positions. As the branch develops the leaves gradually become more and more definite in position and in form, and the branch soon acquires the appearance

FIG. 36. *Bazzania Brighami*. Oahu, Hawaiian Islands (C. M. Cooke, Jun.). $\times 40$.

characteristic of the species. Occasionally, as in *Cephaloziella Turneri*, a species of Europe, Africa, and North America, the base of a branch bears underleaves, even although these are absent from fully developed shoots. The modifications mentioned are apparently all reversionary in character.

Intercalary branches arising from ventral segments are far more common than those just described and have been less subject to discussion. Certain genera, such as *Herberta*, *Anastrophyllum*, and *Saccogyna*, seem to branch invariably in this way, and the same thing is true of many species of *Cephalozia* and *Odontoschisma*. In other cases ventral branches of this type occur in connexion with lateral intercalary branches, as in *Cephaloziella Turneri*, or with terminal branches, as in the genera *Lepidozia* and *Bazzania*. When found in connexion with lateral branches the ventral branches are usually specialized in some way. In *Lepidozia*, for example, the ventral branches are almost always sexual, while in *Bazzania* they are mostly sexual or flagelliform. Even in this latter genus, however, ventral branches with normal leaves are occasionally produced, and Fig. 36, which is drawn from

the Hawaiian *B. Brighami*, shows a branch of this kind and may be considered as representative of ventral intercalary branches in general. These branches, as Leitgeb long ago pointed out, are usually situated in the axils of underleaves or in corresponding positions in species where underleaves are not formed. In the example figured it will be noted that the underleaf with the axillary branch is strongly reflexed.

There seems to be no definite sequence in the leaves of a ventral intercalary branch; neither is there any apparent relation between the spiral of a branch and that of the branching axis. The modifications present are similar to those described under lateral branches. Although ventral branches of this type usually occur singly in the axils of underleaves, in certain genera, such as *Calypogeia* (*Kantia*), two or three of them are sometimes found side by side. In other cases, such as *Cephalozia bicuspidata*, a branch may develop from any part of a ventral segment. Sometimes branches of this character arise directly from fully differentiated cortical cells and are thus destitute of basal sheaths. Such branches are to be regarded as adventive rather than as intercalary, although the distinctions between the two are not always hard and fast. Adventive branches in this position are essentially like those which sometimes spring directly from leaf-cells. They represent a type of regenerative process and scarcely come within the scope of the present paper.

Subfloral innovations in *Radula*, *Fubula*, and the *Lejeuneae* have already been spoken of in connexion with the *Radula* type of branching. They apparently arise whether fertilization has taken place or not. In many plants with intercalary branching subfloral innovations are also found, but their development, in certain cases at least, is dependent upon an absence of fertilization. Such innovations, which seem to be always intercalary in origin, usually occur singly, although groups of from two to four are not infrequent in certain species. They arise both in lateral and in ventral segments, the latter position being somewhat more common. The innovations are usually more robust than other intercalary branches, but show no further distinctive characteristics.

General Considerations.

From his study of the various types of branches in the *Jungermanniaceae*, Leitgeb ('75, '77) reached the conclusion that they had made their appearance in a definite phylogenetic sequence. He believed that branches of the *Frullania* type came first, that these were followed by branches of the *Radula* type, and that intercalary branches came last. He obtained support for these ideas not only from the *Jungermanniaceae* themselves but also from the *Metzgeriaceae*, the branches of which he homologized with those of the *Jungermanniaceae*. In the more primitive *Metzgeriaceae*, for

example, such as *Riccardia* (*Aneura*) and *Pellia*, he considered the terminal branching to be essentially the same as that of the *Frullania* type; in more advanced genera, such as *Hymenophyton* (*Umbraculum*) and *Symphygyna*, he distinguished terminal branches of both the *Frullania* and the *Radula* types; while in the ventral sexual branches of *Metzgeria* and *Hymenophyton* he found typical intercalary branches comparable with those of *Lepidozia* and *Cephalozia*. In the Metzgeriaceae, therefore, there is at least a vague indication that the types of branches which he regarded as the more recent are associated with genera which show other advanced characteristics.

If it is assumed that the Jungermanniaceae are descended from some thallose member of the Metzgeriaceae, it would be natural to conclude that the various types of branches were among the characteristics directly inherited. The probability of a polyphyletic origin of the Jungermanniaceae must, however, be kept in mind, especially in view of the fact that the leafy genera of the Metzgeriaceae are doubtless descended from more than one thallose ancestor. There is some evidence, for example, that the Jubuloideae (of Schiffner) are descended from the Metzgerioideae, while the Epigoni-antheae came from such genera as *Pellia* and its allies. If this is the case it is of course possible that some of the primitive Jungermanniaceae came from thallose ancestors showing only one or two of the types of branching characteristic of the Metzgeriaceae as a whole. The result would be that the lines of development commenced by such primitive forms would either lack the types of branches which they failed to inherit or would acquire them independently. Probably both courses were pursued by different evolutionary lines. If it is admitted, therefore, that the branches appeared in the sequence indicated by Leitgeb, it must also be admitted that this sequence may have appeared in various distinct phyla.

Aside from the unsatisfactory phylogenetic evidence just brought forward, there is also ontogenetic evidence supporting Leitgeb's ideas of sequence. In a species where several types of branching are present it will be found that terminal branching tends to appear first in the life-history of an individual plant, and that branches of the *Frullania* type tend to come before those of the *Radula* type. This is well illustrated by both the Jungermanniaceae and the Metzgeriaceae. In *Lepidozia* and *Metzgeria*, for example, the terminal vegetative branches precede the sexual intercalary branches, while in *Bryopteris* the vegetative branches of the *Frullania* type precede the sexual and flagelliform branches of the *Radula* type.

Leitgeb concluded further that the various types of branches were genetically related to one another. He considered that the *Radula* type was derived from the *Frullania* type through a delay in the process of branch formation, and that intercalary branches represented the culmination of this tendency to delay. Even if the importance of such a tendency as an evolutionary factor is recognized, it is difficult to understand how one type

of branching can have been directly derived from another. Ordinarily, when two organs are genetically related, they are alike at the beginning and acquire the differences which they show at maturity during the course of their development. In other words they represent diverging lines. This is clearly seen in such organs as the scale leaves and the foliage leaves of the higher plants, the earliest rudiments of which are quite indistinguishable. In dealing with structures of this kind, Goebel ('98-'01, p. 577) has shown by experiment that it is possible to alter the course of development of a particular rudiment. He has shown, for example, that a rudiment, which from its position on a growing point would normally develop into a scale leaf, can be acted upon in such a way that it will develop into a foliage leaf instead. Nothing of the sort is conceivable with regard to the branches of the Jungermanniales. These show their distinctive differences at the beginning and tend to become more and more alike as development proceeds. Instead of representing diverging lines of development they represent converging lines (except in cases of marked specialization), and it would be quite impossible to convert a young branch of the *Frullania* type into a branch of the *Radula* type. To do so would necessitate a change in the position of the first branch-segment or else in the direction of the branch-spiral, either of which would of course be out of the question. On the whole it seems most logical to consider the differences in the branches as really due to mechanical causes, which in some way determine the position of the first branch-segment and the direction of the branch-spiral. This would obviate the necessity of looking for a genetic connexion between the various types.

The development of a branch is undoubtedly to be looked upon as a response of the shoot to some kind of a stimulus. The different kinds of branches might then be due to the same stimulus acting upon segments of different ages or to distinct stimuli. To a certain extent at least the latter hypothesis seems to correspond better with the facts, and there are even reasons for believing that intercalary branches in different positions may sometimes be induced by unlike stimuli. These ideas are best supported by the study of species in which branching is a more or less unusual phenomenon. To illustrate the conditions under which terminal branches are developed *Cephalozia bicuspidata* may be selected, while *Plagiochila Sullivantii* and *P. asplenioides* may be chosen to illustrate intercalary branching.

In *Cephalozia bicuspidata* it will be found that terminal branching is not only associated with exceedingly young segments and with young individual plants, but that the conditions necessary for a vigorous vegetative development must be present before the appearance of such branching can be induced. Under ordinary circumstances, therefore, a plant will go through life without branching at all until the characteristic intercalary

branches are formed. The plants discussed in the present paper, however, grew in places where there was an abundant water supply, together with the other factors favourable for growth. Apparently, in response to these conditions, terminal branches are of frequent occurrence. It would appear as if the increased stimulus for growth had acted upon some of the young segments in the same way that it acted upon the apical cell of the shoot, the result being that new apical cells became differentiated in the segments and thus gave rise to new terminal branches.

In *Plagiochila Sullivantii* and *P. asplenoides* the leafy shoots represent branches of a prostrate caudex. These shoots continue growing for a considerable period but usually remain unbranched. It will be found, in fact, that the very conditions which induce a vigorous apical growth and terminal branching in *Cephalozia bicuspidata* tend to inhibit the formation of intercalary branches in these species of *Plagiochila*. It is only when the apical growth is diminished or brought to an end, perhaps through the enfeeblement or death of the apical region, perhaps through the production of archegonia, that intercalary branches can make their appearance. Even under these circumstances branching rarely occurs. In his interesting researches on regeneration in the Hepaticae, Kreh ('09, p. 249) has recently brought out an important fact about *P. asplenoides* (and certain other species). He finds that, when fragments of a shoot are placed under favourable conditions, the regenerative branches appear in the axils of the leaves, that is, in the position where intercalary branches would normally occur. Of course, under these circumstances, the inhibitory action of the apical region has been rendered ineffective by direct removal. From these various observations it would appear that intercalary branches are not only associated with old segments and mature plants, but that the stimulus inducing branch-formation of this type must be distinct from the stimulus which induces a vigorous growth of the shoot, and therefore distinct also from the stimulus which causes terminal branching in such a species as *Cephalozia bicuspidata*.

Terminal branching in *Lophozia* is due to stimuli which are apparently similar to those indicated in the case of *Cephalozia bicuspidata*. In *L. Wenzelii*, for example, branches of the *Frullania* type are not infrequent. The plant grows in cold bogs and is therefore under favourable conditions for vegetative growth. In the closely related *L. alpestris*, which grows in drier localities, branching is much more unusual. In this connexion *Lophocolea heterophylla* may also be mentioned. The juvenile condition in this species, in which the leaves are uniformly bifid, is often greatly prolonged. During this period the conditions favourable for growth are present, and terminal branches occur frequently. As the plant approaches maturity the shoots develop irregularly lobed or undivided leaves, and finally the sexual organs with their bracts. After these changes, associated with repro-

duction and the cessation of vegetative growth, have begun to make their appearance, terminal branches become very rare.

In *Cephalozia*, *Lophozia*, and *Lophocolea* the formation of terminal branches cannot be looked upon as a firmly established habit. Certain species fail to show them at all, and even in species where they may occur it is often possible for an individual plant to go through life and produce organs of reproduction without being stimulated to develop branches of this character. It is very different with such genera as *Frullania* and *Lepidozia*, where the habit of forming terminal branches is firmly fixed. Here the branches arise at fairly definite intervals as long as the conditions necessary for ordinary growth are present. Even here, however, there are a few facts which point to a slight connexion between vigorous growth and branching. In plants growing in dense shade, for example, there are often more leaves between successive branches than in plants growing under more favourable conditions. In branches, also, the growth of which seems to be more or less inhibited by the vigorous development of the main axis, branches of a higher order less frequently occur. It is only when such branches overcome the inhibitory action and assume the characteristics of the main axis that they branch with the same degree of frequency. In the first case the conditions unfavourable for growth (and for branching) are due to an unfavourable environment, in the second case to correlative influences. The second case, however, must not be confused with the one described under *Plagiochila*, where the formation of intercalary branches is inhibited by the growth of the branching axis itself, and not by the growth of an axis of higher rank.

The antagonism between apical growth and intercalary branching, which is shown so clearly by *Plagiochila Sullivantii* and *P. asplenoides*, is usually present even in cases where intercalary branching has become a characteristic habit. To illustrate this point *Cephalozia bicuspidata* may again be selected. The sexual branches in this species, which are commonly intercalary and ventral, make their appearance when a certain degree of maturity is reached. Their development, however, is longer deferred in vigorous plants, and especially in plants so vigorous that terminal branches are present. An important difference between the *Cephalozia* and the two species of *Plagiochila* in this respect is that the antagonism in the *Cephalozia* is less strong, the result being that the inhibitory influence of the apical region is more easily and more regularly overcome.

The ventral flagelliform branches in *Bazzania*, which are also intercalary, stand in marked contrast to the branches just considered, although the sexual branches in the same genus are apparently dependent upon the same conditions as those of *Cephalozia bicuspidata*. These flagelliform branches make their appearance only a short distance away from the apical region, and there is no evidence that their development is inhibited by

apical growth. In fact the stimulus which induces growth and the stimulus which induces branches of this character apparently act in harmony. From the consideration of this peculiar case, therefore, it seems very probable that the stimuli inducing intercalary branching are not always identical.

Summary.

Two distinct kinds of branching, terminal and intercalary, may be distinguished in the Jungermanniaceae. In terminal branching the branches arise in very young segments; in intercalary branching they arise in segments which are more or less mature.

Terminal branching includes four distinct types, characterized by the portion of the segment which takes part in branch formation. These four types are here designated the *Frullania* type, the *Microlepidozia* type, the *Acromastigum* type, and the *Radula* type, respectively. In the *Frullania* type the branch represents the ventral half of a lateral segment; in the *Microlepidozia* type, the dorsal half of a lateral segment; in the *Acromastigum* type, one of the halves of a ventral segment; in the *Radula* type, a portion only of the ventral half of a lateral segment.

In the *Frullania*, *Microlepidozia*, and *Acromastigum* types the branch is always accompanied by an incomplete leaf, which represents the other half of the same segment; in the *Radula* type the branch is accompanied by a complete leaf, which belongs to the same segment.

In the *Frullania* type the first branch-segment is ventral, and usually gives rise to an underleaf, the second segment is acroscopic (with respect to the branching axis) and gives rise to the first lateral leaf, while the third segment gives rise to the second lateral leaf, basisopic in position. The branch-spiral is homodromous with the axis when the branch has arisen in an anodic segment-half, and antidromous when it has arisen in a kathodic segment-half.

In the *Microlepidozia* type the third branch-segment is ventral in position, and the branch-spiral is always homodromous with the axis because the branches of this type always arise in anodic segment-halves.

In the *Acromastigum* type the third branch-segment is ventral (just as in the *Microlepidozia* type), and the branch-spiral is homodromous or antidromous with the axis, according to whether the branch is situated in the anodic or the kathodic segment-half.

In the *Radula* type the first branch-segment is sometimes ventral, but usually lateral and basisopic. The branch-spiral is usually sinistrorse on the left-hand side of a branching axis, and dextrorse on the right-hand side (when the shoot is viewed from the ventral surface), but subfloral innovations in the Lejeuneae sometimes show variations.

The leaves at the base of a terminal branch, especially one of the *Frullania* type, are more or less modified in form, in size, and in manner of

attachment, some of these modifications representing reversionary tendencies and others special adaptations.

Intercalary branches may be either lateral or ventral in position. Their spirals show little or no relation to the spiral of the branching axis, and there is nothing definite about the position of the first branch-segment. The modifications at the base of a branch are reversionary in character.

There is some evidence (derived from phylogenetic and ontogenetic considerations) that the *Frullania* type of branching was the first one to make its appearance, that this was followed by the *Radula* type, and that intercalary branches came afterwards. It is possible that this sequence appeared independently in different developmental lines. A tendency to delay in the process of branch formation was apparently an important evolutionary factor.

There is evidence also that there is a harmonious relation of some sort between vigorous vegetative development and terminal branching, and that there is usually an antagonism between vigorous growth and intercalary branching.

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